



## Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at <http://about.jstor.org/participate-jstor/individuals/early-journal-content>.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact [support@jstor.org](mailto:support@jstor.org).

THE  
BOTANICAL GAZETTE

NOVEMBER 1917

FOOTHILLS VEGETATION IN THE COLORADO  
FRONT RANGE

CONTRIBUTION FROM THE HULL BOTANICAL LABORATORY 237

ARTHUR G. VESTAL

(WITH EIGHT FIGURES)

The coniferous forests of the Rocky Mountains are fairly well known; the other plant associations have been little studied. In the present account descriptions are given of typical representations of the plant communities of the foothills zone. The area is confined to the eastern slope of the Rockies in Colorado. By the foothills zone is meant the lower elevations, from the plains at 5000-6000 ft. to the middle slopes at 7500-8000 ft. The vegetation zones of the Colorado mountains have been characterized by RAMALEY (10). A large part of the field study has been made in the area just west of Boulder, during three years' residence at the University of Colorado; the other parts of the region have been studied on numerous visits, chiefly to stations at or near the mountain-front, from the Big Thompson River as far south as Raton, New Mexico. This article is the second of a series dealing with the vegetation and plant geography of the eastern mountain-front in Colorado. The first account (24) is of the plains and prairie associations of the region. The writer is indebted to Professor FRANCIS RAMALEY for many kindnesses and for help in different ways.

Grassland in the Rocky Mountains has a much more important rôle than is usually accredited to it, particularly in the lower slopes.

It is perhaps the conspicuousness of the trees, especially in distant views and in profiles of slopes (fig. 8), which gives the common but not wholly true impression that the foothills are generally forested with conifers. The rock pine, the most generally distributed conifer of the region, forms relatively few and scattered true forests; it usually grows in very open formation, in mixture with the grassland which covers most of the surface. The general aspect of the vegetation is that of an open growth of grassland and scattered pines over a dry and partly bare upland of granitic hills. Semi-mesophytic and mesophytic communities, of both herbaceous and woody plants, occur; but only locally, in moister or more sheltered ravines and canyon-bottoms. The vegetation complex of the mountain-front is a modification of that of the foothills, but is less simple in composition.

### **Environmental conditions**

The Front Range in Colorado is an up-arched and dissected plateau of crystalline rocks, the tops of most of the hills forming the remains of a peneplaned surface; scattered higher mountains represent monadnocks surmounting the former general level. The eastern part of the plateau slopes gently toward the plains, the sedimentary strata of which are here upturned against the granitic rocks, forming sloping crags on the outer face of the foothills, or hogback ridges separated from the hills by north-south valleys. The physical geography of the Front Range is described by DAVIS (5). It is with the lower, more easterly part of the granitic plateau and with the more irregular country of the mountain-front that this study has to do.

The climate of the foothill region is dry, though not enough so to be called semi-arid, like that of the plains. Rainfall at the mountain-front is from about 15 to 18 inches average for the year; higher in the northern part of the state and on the elevated Platte-Arkansas divide, lower south of the Arkansas River. The upper foothills receive about 18-20 inches. Annual variation of rainfall is considerable. Most of the rain comes during the growing season. At Boulder, and in the northern foothills generally, April and May are the rainiest months; in the southern foothills the earlier part of the summer is drier than later. This, with higher summer

temperatures and probably greater insolation, gives a drier aspect to the southern foothills; pinyons are abundant, instead of rock pine, as in the northern part of the state. Mean annual temperatures in the foothills vary from 40 to 50° F.; mean summer temperatures 60 to 70° (ROBBINS 17). Evaporating power of the air is great, though much less than on the plains. Local variations in atmospheric conditions, due to surface configuration, are considerable. Insolation is much greater on summits and south-facing slopes than on north-facing slopes or in ravines. The drying winds are usually from the west, and their effects are greatest on summits and the flatter uplands.

Local and topographic factors are extremely and very locally variable. Position with reference to surroundings, and slope, its amount and direction, may perhaps be called the two master factors of the topographic complex. Slope and position are most important in determining conditions of soil deposition or removal (consequently depth and texture of the soil); conditions of absorption and run-off, drainage, or seepage from above, or possible seepage from snowdrifts; presence or absence of plant remains, which may contribute humus, or locally form a mulch (pine needles); and conditions of exposure to sun and wind with its attendant effects. The granitic hills in general (fig. 1) are in an early-mature stage of topographic development (for a mountain region of resistant rocks); the side-slope profiles are nearly straight, with comparatively little detritus covering the bottom of slopes; the tops of the hills are usually rounded, and hardly more subject to erosion than the sides. In general, the foothills are so well drained that bogs, marshy flats, and moist-soil meadow areas are infrequent, even in canyon-bottoms. Hilltops and side-slopes are covered, usually thinly, with rock-débris or with decomposed granite soils, varying in texture from coarse gravelly material of angular fragments<sup>1</sup> to fine black loamy humus. Wide dikes and occasional outcrops of more resistant rock have only a little soil, in joints and crevices, hardly any elsewhere.

<sup>1</sup> The writer has not been able to find a distinctive name for this coarse angular débris resulting from decomposition of granite; it is not gravel in the sense the word usually implies; in this article it will be called "granite-gravel."

Texture of soil in its influence on water relations is probably the most important soil factor in the foothills, so far as local distribution of plants is concerned. Especially interesting are some of the features of mixed soils, in which fragments of greatly different sizes are intermingled. Rocks of all sizes may occur on the surface, or buried among finer fragments as rock-débris of detrital slopes. Where the large fragments are imbedded beneath the surface in fine soil, the water content of the latter appears to be increased.

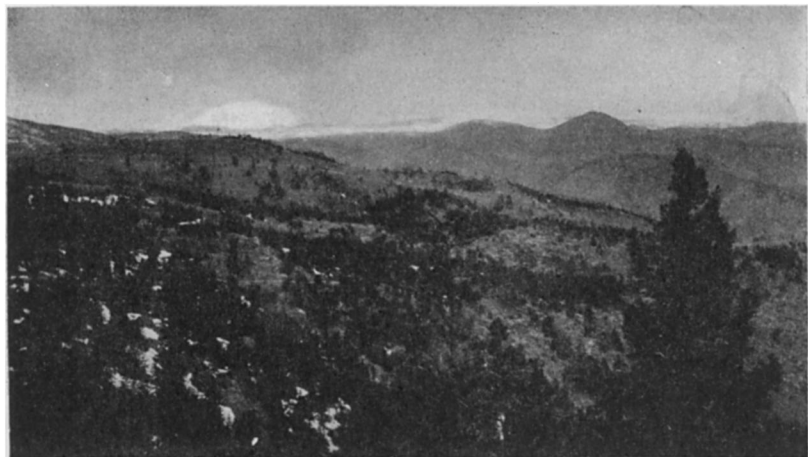


FIG. 1.—General view in foothills, looking westward to snowy range-crest; foreground a north slope; general vegetation grassland with scattered pines; southwest of Boulder, 7200 ft.

Where the large rocks are exposed at the surface, moisture conditions appear to be more favorable immediately beside and under them, so that comparatively mesophytic plants are seen growing in mixture with xerophytes, the former always growing beside or from under the surface rocks. This effect will be noticed in the lists of species; many plants are found in both xerophytic and mesophytic assemblages.

The more frequently recurring combinations of topographic and atmospheric factors which form effectively different local environments for plants may be viewed in the synopsis which follows. It is intended to apply only to the foothills proper; a number of situations of the mountain-front belt cannot be included herein.

## CLASSIFICATION OF FOOTHILLS HABITATS

Xerophytic habitats (the general condition of summits and side-slopes)

Rocky habitats

Craggy summits and rock-walls (see figs. 2, 3)

Rock-strewn detritus slopes

Rock-talus, usually less stable than preceding

“Granite-gravel” habitats

Compacted granite-gravel floors and side-slopes (see fig. 3)

Loose granite-gravel floors, washes, and talus (= gravel slides)

Fine-soil habitats

Mixed-soil floors and detritus-slopes (fine soil with imbedded and superficial rock fragments of various sizes)

Fine-soil floors and detritus-slopes (infrequent)

Less xerophytic habitats (valleys and steep slopes, etc., relatively local)

Less xerophytic side-slopes (mostly north-facing, usually of considerable gradient, and best developed in valleys)

Mesophytic ravine habitats

Narrow ravines (best developed in small side-canyons, especially on the south side of eastward-flowing main streams)

Canyon-bottoms (the wider bottoms of the larger canyons are sometimes, however, exposed and xerophytic)

Seepage and dripping areas (infrequent and small)

Stream-side habitats (with usually constant supply of soil moisture, but widely varying atmospheric conditions)

## Synopsis of plant associations

The following synopsis is aimed to give in perspective the distinguishing characters of the plant communities of the foothill region. It is based upon whatever features of the particular community seem most distinctive and appropriate: growth-form, moisture relations, physiographic, geographic, and successional relations.

## CLASSIFICATION OF FOOTHILLS ASSOCIATIONS

Associations generally primitive in character: the first vegetation of new or unfavorable habitats, usually in rocky or gravelly situations; vegetation open and sparse, generally xerophytic

Plants lichens; on rock surfaces, either on craggy summits, knobs, and rock-walls, or on loose boulders.....*Lichen associations*

Plants spermatophytes, in rocky or detrital situations, soil of variously coarse texture

Dominant plants shrubs; of relatively local and temporary occurrence; frequent in areas recently denuded.....*Sumac association*

Dominant plants herbaceous.....*Foothills primitive grassland association*

Associations generally intermediate or established in character (usually subsequent to primitive associations, but often in habitats apparently little modified from the primitive condition); soil often of mixed or fine texture, or with considerable humus content; vegetation usually less open and sparse than in preceding

Typically developed in xerophytic or semi-xerophytic habitats, which are of general occurrence in the foothills region (these associations are consequently extensive)

Dominant plants evergreen trees; usually in rocky or coarse soil

Of relatively less xerophytic character; generally distributed in the foothills region. . . . . *Rock pine association*

Of relatively more xerophytic character; of lower and (east of the range-crest) more southerly distribution than preceding

*Pinyon-cedar association*

Dominant plants deciduous trees or large thicket-forming shrubs; of southerly distribution east of the range-crest; frequent in fine soil, and ranging into less xerophytic habitats. . . . . *Quercus association*

Dominant plants shrubs

Shrubs tall and loosely branched, occurring mostly at and near the mountain-front, in coarse or rocky soils. . . . . *Cercocarpus association*

Shrubs low, creeping and densely branched, occurring mostly in the foothills proper

Plants evergreen, of northerly distribution, more frequent in the higher foothills. . . . . *Arctostaphylos association*

Plants deciduous, of more southerly distribution, more frequent in the lower foothills. . . . . *Ceanothus association*

Dominant plants herbaceous; vegetation grassland, composed mostly of xerophytes

Dominant plants including plains short-grasses of surface-rooted habit; plant population large and diverse, *Foothills mixed grassland association*

Dominant plants mostly tufted bunch-grasses of deeper-rooted habit

*Bunch-grass association*

Typically developed in mesophytic or semi-mesophytic habitats (which are much less extensive in the foothills than xerophytic habitats, being represented chiefly on north slopes and in ravines and canyons)

Dominant plants evergreen trees. . . . . *Pseudotsuga association*

Dominant plants deciduous trees

Typically developed along stream margins in open canyons

*Populus-Salix stream-side association*

Typically developed in less exposed situations than preceding, as bottoms of v-shaped ravines and moist shaded slopes

*Canyon forest association*

Typically developed in moist ravines or slopes with humus soil; or, in the higher foothills, in moist patches of the granite-gravel upland

*Aspen association*

Dominant plants shrubs, or rarely reaching tree size

Plants larger, comparatively well separated; plant composition variable; ranging also into xerophytic habitats

*Foothills mixed shrub association*

Plants smaller, low, closely set, usually in fine moist soil

*Symphoricarpos association*

Dominant plants herbaceous . . . *Foothills mesophytic grassland association*

### Descriptions of associations

The plant communities are described in the order of their appearance in the foregoing synopsis. They are subject to greater geographic variation than can be treated fully in this article; mention is made, however, of the more considerable variations. The space allotment is not always proportionate to the importance or general interest attaching to the several associations; some are already fairly well known, some are less variable or can be summed up more concisely than others, and some have been less thoroughly or less widely studied. An approach to a balanced treatment has been sought by the use of a smaller type for statements of less general significance, descriptions of minor or very local vegetation divisions, and detailed passages included by way of illustration or amplification.

Plant names, when appearing without citation of authorities, may be understood to be as in COULTER and NELSON's *Manual* (2), which in general follows the usage recommended by the Vienna Congress. The unit of vegetation is the plant association, in the generally accepted sense; its distinctive representations, appearances, or variants are spoken of as consocieties; the terms as used are described in an earlier article (24, p. 382, footnote). Index letters attached to species names signify frequency or abundance or regularity of occurrence, as follows: *a*, abundant; *f*, frequent; *i*, infrequent; *l*, local or locally; *ch*, characteristic in the community or situation mentioned.

It will be understood that the total number of species of plants occurring in an area so extensive as that of this study is very large. No attempt has been made to work out the complete floristics, or the floristic variation of the several communities as represented in different localities. Field botanists will remember that very many of the species making up the flora of a region are rare, known from a single or very few stations, are in effect of very slight ecological significance, so far as vegetation is concerned. A further considerable proportion is not found in extensive plant assemblages (as, in this study, grass species occurring only in stream margins), and is not important as part



of the vegetation of the general area. Several or numerous species of certain genera, again, may be of similar habitat distribution, so that a species of one locality may be replaced in the same habitat in another locality by a second species of that genus. Care has been taken to select species for the floristic lists which are as representative over a considerable area as may be. In the southern foothills, as in the plains of southern Colorado, many more plants of southwestern derivation enter into the flora, particularly in the primitive grassland and mixed grassland assemblages. Many are true desert plants; a few cacti and chenopods and many composites fall in this group. That this geographic variation from north to south is ecological as well as floristic should be apparent. It is paralleled by a similar altitudinal variation in composition, from the montane zone to the plains.

#### LICHEN ASSOCIATIONS

TUCKERMAN (23); WILLIAMS (27), lichens in the Black Hills; HERRE (7), lichens of Mount Rose, Nevada; SHANTZ (22, p. 187).—Fig. 2.

A considerable proportion of the area of the foothills is exposed rock, and its vegetation, except in crevices, is mostly composed of lichens. The study of lichen vegetation has usually been left to the specialists in that group of plants, since they are so poorly known to most other botanists. For this reason brief notes on external appearance, as to color and vegetative form, are given with the species names. The writer is indebted to R. HEBER HOWE, Jr.,<sup>2</sup> who has made the species determinations and examined this part of the manuscript (fig. 2).

*Dry surfaces, much exposed to sun and wind*, occupy most of the area of bare rock in the foothills. They slope considerably, so that run-off is rapid and absorption minimal. The first lichens to invade dry rock, forming primitive xerophytic stages of lichen growth, are fine-grained crustose forms, notably the black-gray *Rinodina radiata* Tuck. (? = *R. thysanota* Tuck.) and an indeterminate lead-gray species which is especially characteristic. These are soon followed, but not displaced, by lichens of an intermediate stage, mostly coarser crustose forms; the gray-green *Rinodina oreina* (Ach.) Wain. is a character species both locally and geographically abundant. The established stage on dry rock is marked by the gray-green small-foliose *Lecanora rubina* (Vill.) Wain. and the

<sup>2</sup> Some of the crustose species were determined for Dr. HOWE by H. E. HASSE; the *Stereocaulon* by L. W. RIDDLE.

larger-foliose, also gray-green, *Parmelia conspersa* (Ehrh.) Ach., which may be said to be the dominant and most frequent lichen of exposed rock. Here also occur the gray-green crustose-foliose *Rhizocarpon geographicum* (L.) DC., with *Rinodina oreina* persisting from the preceding stage, and a few other species, including one or two of *Parmelia*, *Gyrophora erosa*, and the large and peculiar *Gyrophora vellea* (L.) Ach., in crisped-margined dirty-gray plates 0.25–2 inches in diameter, attached centrally beneath. These



FIG. 2.—Lichens on steep rock-wall of rather sheltered side-canyon opening northward into Boulder canyon; dark masses at joints are cushions of *Selaginella*.

established stages appear to be self-perpetuating so long as physical conditions of dry rock are unchanged.

*Less exposed, but usually dry, surfaces*, such as shaded rocks, overhangs, surfaces dripping for some time after rains, recesses in joints, etc., have also characteristic lichen assemblages and definite successions. The earlier lichens include the yellow-green crustose *Acarospora xanthophana* (Nyl.) Fink (characteristic and abundant), with *Lecanora rubina*, *Rhizocarpon geographicum*, and *Rinodina radiata*. *Acarospora* persists in the established stages, which also show the bright orange-brown crustose-foliose *Caloplaca elegans* (Link.) Th. Fr. (characteristic and abundant), *Parmelia conspersa*, *P. sulcata* Tayl., *P. conspersa* var. *stenophylla*? Ach., *Gyrophora vellea*, and other species. Considerably less of the rock surface remains uncovered with lichens here than in the xerophytic situations, and the number of species is larger, although the area of this

habitat and its lichen assemblage is very much smaller. *Caloplaca elegans* and *Parmelia sulcata* are frequent on scattered rocks and tree trunks in shaded canyon-bottoms.

*Moist surfaces* in humid recesses of the rocks show numerous lichen species, mostly foliose, including *Physcia aiopolia* (Ach.) Nyl. and a number of species of *Parmelia*. Mosses grow with the lichens abundantly in these situations. These distinctly humid recesses are scattered and infrequent in the foothill region. A *Cladonia*, probably *C. fimbriata* (L.) Fr., is characteristic on moist north-facing canyon slopes, amongst mesophytic herbs, or beside surface rocks. A pulvinate, finely divided whitish fruticose lichen, *Stereocaulon albicans* Th. Fr., has the growth-form of a pulvinate moss, being "rooted" in moist rock crevices, although the aerial part is more or less exposed. It is infrequent.

#### SUMAC ASSOCIATION

ROBBINS (16, p. 46), distribution on Long Mesa near Boulder.

As indicated in the synopsis of associations, the shrubs of sumac (*Rhus cismontana* Greene, which is so like *R. glabra* of the eastern states as to be considered identical with it by some botanists) often form a new plant assemblage in denuded xerophytic situations. These are extremely variable, including old roadways, rock talus below road embankments, quarries, or prospect holes, stony hillsides where erosion or landslipping has removed much of the plant cover, or places which have been burned. In the lower foothills, and at the mountain-front, the sumac appears to be quite common after fires, the slopes being too dry to allow the establishment of aspens, in most places. The shrubs are usually separated, the sparse plant cover of the interspaces often being composed of plants of the primitive grassland association. As developed in the foothills, the assemblage shows no essential difference from the sumac growths of many parts of the United States. In autumn the bright red coloring of the leaves makes the community very conspicuous, so much so as to give an exaggerated notion of its frequency of distribution.

#### FOOTHILLS PRIMITIVE GRASSLAND ASSOCIATION

CLEMENTS (1, pp. 9-12), gravel slide formation, half gravel slide formation, in part; RAMALEY (12, pp. 124-128), *Cercocarpus* scrub, upland dry grass, and foothill sagebrush-grass formations, in part; SCHNEIDER (21), gravel slide and half gravel slide formations, in part.

The principal herbaceous growth of dry coarse-soil situations in the foothills presents very great variability, and is very generally distributed, occupying not only large areas by itself, but occurring in mixture with shrubs and trees representing different associations. It is perhaps not too much to say that only a small proportion of

the area in which the rock pine is of frequent occurrence is occupied by actual forest; the usual vegetation of the pine-sprinkled upland is open, the ground-cover is made up of associations of herbaceous plants or low shrubs; prominent among these is the primitive grassland. It enters largely into the ground-cover of other mixed associations also, in which trees and shrubs other than rock pine are conspicuous. The variability of such an open ground-cover as the primitive grassland is so great that no particular set of plants can be said to characterize the whole community, although certain features are common to all of its variants or consocieties: (1) they constitute the first vegetation in new and unfavorable habitats; (2) this vegetation is sparse and open; (3) it is made up of an assemblage of species typical of coarse soils and rather considerable exposure to sun and wind, some more commonly in the plains, others in the mountain region (many of these plants are common to several of the consocieties, though some few are typical only in the more extreme developments of particular consocieties-habitats, as *Erigeron compositus* in packed granite-gravel); (4) as development of vegetation proceeds in the several consocieties, with accumulation of the plant remains, closing of the plant cover, etc., they resemble one another more closely, converging into a less open growth, which may be known as the foothills dry grassland association, the next higher in the genetic series. Many of the species of the primitive grassland seem not to be particularly xerophytic, as *Thlaspi coloradense* and *Gilia aggregata*, for these are active during the early part of the season, when the moisture supply is ample. Such plants are very widely distributed in the foothills and are not characteristic of particular habitats nor of the species groupings of particular plant communities.

A partial list of species of the primitive grassland follows:

SPECIES LIST: PRIMITIVE GRASSLAND

Selaginella densa ( <i>l</i> )	Phlox multiflora
Aristida longiseta ( <i>l</i> )	Gilia aggregata
Stipa comata ( <i>l</i> )	Gilia pinnatifida
Bouteloua hirsuta ( <i>l</i> )	Phacelia heterophylla ( <i>ch</i> )
Koeleria cristata ( <i>ch</i> )	Oreocarya virgata
Sitanion brevifolium ( <i>l</i> )	Pentstemon humilis

Arenaria Fendleri	Chrysopsis villosa ( <i>ch</i> )
Paronychia Jamesii ( <i>ch</i> )	Chrysopsis spp. ( <i>ch</i> )
Berberis aquifolium	Townsendia exscapa
Thlaspi coloradense	Townsendia grandiflora
Physaria floribunda ( <i>l</i> )	Machaeranthera aspera
Lesquerella montana	Helianthus pumilus
Sedum stenopetalum ( <i>ch</i> )	Hymenoxys floribunda (south)
Potentilla pennsylvanica strigosa	Gaillardia aristata
Potentilla Hippiana	Artemisia frigida ( <i>ch</i> )
Astragalus Purshii	Artemisia gnaphalodes var. ( <i>ch</i> ) <sup>3</sup>
Geranium Parryi ( <i>ch</i> )	Senecio Nelsonii ( <i>ch</i> )
Mentzelia spp.	

The more important representations of the association in special habitats:

(1) The mixed consocieties of mixed detrital slopes. This term may be applied to the very sparse plant community of slopes on which the fragments of rock-débris are of all sizes, and in which as a result conditions for plant life vary extremely locally. The vegetation may be regarded as a mosaic of different variants of primitive grassland, with the addition of certain components from other vegetation types, as the lichen, shrub, and pine associations (see figs. 4, 8).

(2) The *Geranium-Chrysopsis* consocieties of unstable granite-gravel slopes, in which the loose bunches of these two plants are the most frequent or the only plants in the loose decomposed granite soil.

(3) The *Artemisia frigida-Koeleria* consocieties of stony detrital slopes (rock talus, frequently). The habitat is quite common though seldom very extensive; the sage may be very abundant without the grass *Koeleria*; it is an important species in the northern Great Plains and in the mountains up to 10,000 ft.

(4) The compacted granite-gravel consocieties. Dwarfed plants of *Erigeron compositus*, *Senecio Nelsonii*, and a few other species are characteristic in level or gently rolling top surfaces, on which the thin coarse soil has become compacted into a hard floor (fig. 3). In its most extreme condition seen, the *Erigeron* was the only plant, occupying less than 4 per cent of surface. Rather infrequently, *Potentilla Hippiana* occupies these situations, forming a pure growth which spreads vegetatively.

(5) The mat consocieties of gravel slides. These habitats are more frequent in the Pike's Peak highland than in the Front Range proper, where they are

<sup>3</sup> This plant has narrow pinnately 5-divided leaves, and appears to be quite constantly different from the entire or apically 3-divided form with dense white canescence. With this structural difference is an apparently constant habitat difference; the dissected form is usually in very coarse soil, the other in clay, abundant only at the mountain-front. It is hoped that experiments can be made on these to determine whether the forms are genetically distinct, as they are ecologically.

best developed on south-facing slopes, commonly at the bottoms of open canyons, beside graded roadways. Species of *Gilia*, *Physaria*, *Phacelia*, *Berberis*, *Gaillardia*, and *Pachylophus* are characteristic. Gravel slides have been studied by CLEMENTS, and by SCHNEIDER (21).

The primitive grassland is closely related to certain associations of the Plains region, notably the mat association (9, p. 376; 24, p. 393), and the *Gutierrezia-Artemisia* association (24, p. 398), and to the other primitive assemblages leading to short-grass. It is more generally distributed, as would be expected, at lower elevations



FIG. 3.—Granite-gravel floor, with much bare surface, some primitive grassland, and mats of *Arctostaphylos*; in background rocky summit or knob, with scattered pines; Flagstaff Mountain.

and more southerly parts of the mountain region, and in the more exposed habitats. It probably occupies a larger proportion of the total area in the lower parts of the Front Range than any of the other associations in their unmixed condition.

#### ROCK PINE ASSOCIATION

CLEMENTS (1); RAMALEY (10, 12, 14); ROBBINS and DODDS (18), distribution of conifers on the mesas near Boulder; SHANTZ (22, p. 184); WATSON (25, p. 207); YOUNG (28, p. 337).

*Pinus scopulorum*, variously called the rock, western yellow, or bull pine, is the important tree in the foothills. Its plasticity

is remarkable, growing in all kinds of soil, on slopes of every angle and every direction, through wide variations in soil moisture, evaporation, light, and temperature. Its wide geographic and altitudinal range is an expression of this plasticity. In favorable situations it grows rapidly, with straight trunk and branches regularly arranged; in the more exposed places it is reduced in size, and commonly gnarled and irregular. Distribution of the pines is largely a matter of establishment, since the critical stages are seed burial, germination, and the young seedling period. Crevices and soil-filled spaces between rocks, usually of small area, afford lodging places for the seeds; exposed summits and slopes of fine soil are mostly covered with grassland. Small areas of soil deposition may allow burial of many seeds, and consequent development of dense young stands. Seeds germinate well in the tangled mats of *Ceanothus Fendleri* (see under *Ceanothus* association). The first few years of the seedling are safely passed only when several favorable seasons are successive (at least in exposed situations), as shown by RAMALEY (13, p. 30) for the high mesas near Boulder.

According as establishment is abundant or very sparse in a given station, the growth is closed, giving a true pine forest, or scattered, resulting in the well known open or parklike appearance; this is a mixed vegetation of which the pines form only one component. They may later dominate the whole area if new pines can germinate beneath, but on the whole the closed pine forest is relatively infrequent. Just how important an influence in the foothills fire has been, and is, is very difficult to determine; it is said by some residents that the whole region just north of Boulder Creek was once much more extensively forested than now; but if fire is of fairly frequent occurrence in a region, it is an environmental factor to be taken into account. Its effect is wholly favorable to the grasslands and primitive growths, at the expense of the pines (fig. 4).

In the lower and more southerly parts of the foothills, dry grassland and particularly primitive grassland form the ground cover in most areas of scattered pines. The spiny shrub *Ceanothus Fendleri* is also commonly seen between the trees. Away from the individual trees, and often even at their very bases, the plant cover is mostly not different from its condition where

there are no pines. The trees frequently do modify conditions of growth for ground plants, however, where pine needles accumulate, but this effect is very local. Farther up, and to the north, and apparently more closely associated with pine growths, the bearberry (see under *Arctostaphylos* association) is an important part of the ground-cover between scattered trees.

*Juniperus scopulorum* is an infrequent though locally conspicuous tree species found with the pines. *Pseudotsuga mucronata* also mixes in to some extent, even in a few fairly xerophytic stations. *Juniperus communis sibirica* is a ground shrub of infrequent occurrence. *Pinus flexilis* is very locally represented, although not confined to the foothills. *Pinus Murrayana*, the



FIG. 4.—Shallow ravine head; mostly grassland, with fine soil at bottom, and thinner and rockier soil on side-slopes; in coarse soil are numerous pines and *Arctostaphylos* (foreground); in middle ground a considerable clump of *Prunus demissa* (leafless condition), occupying soil moist from seepage; April 1914.

lodgepole pine, of the montane zone, mixes with the rock pine in the upper foothills. The rock pine is by no means absent from the montane zone, and is even quite abundant there if the lodgepole is absent, as in the Pike's Peak highland generally.

The pine association in its unmixed form (practically closed forest) has very few open spaces. Natural pruning of the lower branches is general. Old needles strew the ground; the light is much reduced; the two influences, mulch and shade, acting together or singly, exclude practically all ground plants from the closest stands, and all but a few from less dense forests. Plants of primitive grassland very seldom persist in shade. Relics of former vegetation are seen in less advanced stages, including occasional plants of *Opuntia*, *Cercocarpus*,



bunch-grasses, and others. A few species commonly found in the undergrowth of unmixed but not densely shaded forest are *Harbouria trachypleura*, *Aletes acaulis*, *Senecio* (one or two spp.), *Solidago* (several spp.), and *Pentstemon humilis*.

#### PINYON-CEDAR ASSOCIATION

CLEMENTS (1, p. 8), foothill woodland formation; SHANTZ (22, p. 184); WATSON (25, pp. 205-207), cedar and pinyon formations.

The pinyon, or nut pine, *Pinus edulis*, and less abundantly the cedar of the southern Rockies, *Juniperus monosperma*, are conspicuous plants in the mountain-front of the southern part of the state and in the adjoining foothills. Toward the south conditions are generally more xerophytic at the mountain-front; there the rock pines are common only in higher elevations; they are replaced below by the pinyon. Like the rock pines farther north, the pinyons show local extension eastward into the plains, in rocky habitats, such as the canyon-walls of rock outcrops, and the bluff-crests of the plains stream valleys.

Between the trees are plains or semi-desert plants, many southerly species being present which are rare or absent farther north than about Colorado Springs. One of the most notable of these is the candlestick cactus, *Opuntia arborescens*, common at the mountain-front on rock-strewn slopes and mesas.

The pinyons (and to a smaller extent the cedars) are typically broadly rounded, the diameter of the crown being usually as great as the height of the tree, which is rarely more than 12-15 ft. The trees are usually separated so that the crowns are distant from each other by a diameter or a little less, in the closer stands. The writer has never seen a really closed pinyon forest in which the crowns would form a continuous canopy. The interval between trees increases with xerophytism and exposure, and the branches are less symmetrically developed. Where the habitat is extensive, the pinyons are quite uniformly dotted over the general area. On rocky ridges and mesa-crests the trees are in ragged lines, in small clumps, or irregularly scattered.

#### QUERCUS ASSOCIATION

CLEMENTS (1, p. 6) and SHANTZ (22, p. 179), foothill thicket formation, in part; WATSON (25, pp. 207-210), white oaks in the yellow pine association.

East of the range-crest oaks may be seen nearly as far north as Denver; however, they form more extensive growths to the southward. North of the Platte-Arkansas divide they are perhaps more abundant at the mountain-front and in the Plum and Cherry Creek

valleys than in the foothills proper; they range into finer soils than do the pines. In the foothills as well as at the mountain-front the oaks may share mixed rocky slopes with local representations of *Cercocarpus*, pinyon, rock pine, or grassland associations, or may alternate with them. The extent to which they replace the rock pine on south-facing foothill slopes is appreciable even north of Perry Park, and is increasingly considerable southward. There is no apparent reason why they would not grow north of their



FIG. 5.—Alternation of mixed grassland and oak forest, west of Castle Rock, July 1913; tall herbs conspicuous at border.

present limits in the mountain-front; some of them extend north on the west side of the range-crest even into Wyoming (fig. 5).

The taxonomic condition of these oaks is one of confusion. RYDBERG'S *Flora of Colorado* (19) lists 11 species, all occurring at or near the eastern mountain-front. *Quercus Fendleri* appears to be distinct, much more xerophytic, more southerly in distribution. The intergradations with most of the others are such that specific determinations are very difficult. CLEMENTS mentions *Quercus Gunnisonii* as the chief species of the Manitou vicinity. Certain Colorado botanists now speak of the doubtful oaks collectively, for the present, simply as *Quercus* spp. The writer has thus far not been able to distinguish different habitat groups within these *Quercus* spp. (cf. SHANTZ, 22, p. 179).

So many of the oaks do not reach tree size that the assemblage in many places presents the appearance of chaparral. As might be expected from their wide range of habitat-tolerance, they vary considerably in appearance, from shrubby scattered trees or stunted thickets, to low forest with mesophytic undergrowth. In very favorable stations, as along streams in the southern foothills, the oaks may reach a height of 20 ft. and more. The undergrowth in ungrazed parts of the oak scrub has a decidedly mesophytic stamp during the moister part of the season; *Pulsatilla*, *Castilleja*, *Monarda*, *Calochortus*, *Lupinus*, *Geranium*, *Galium boreale*, *Campanula*, *Thermopsis*, *Danthonia*, *Pentstemon unilateralis*, are typical of oak borders and less densely shaded parts within. Dense closed shaded oak scrub shows abundance of a tall white-flowered umbellifer, *Ligusticum Porteri* (?).<sup>4</sup> Late summer shows many of the less xerophytic composites, including species of *Aster*, *Solidago*, *Erigeron*, and *Brickellia grandiflora* var. *minor*. The undisturbed clumps of small oak trees, where these alternate with dry grassland, are often bordered with tall, rather mesophytic herbs, as *Lupinus argenteus*, *Monarda* spp., and *Achillea millefolium* L. (*A. lanulosa* Nutt.), as may be seen in fig. 5, taken west of Castle Rock.

Low shrubby oak thickets, in grazed areas, are mostly impenetrable to horses and cattle; they are, however, eaten from the outside, and the patches thus slowly reduced in area. This results in a complete replacement of oak by grassland, as stated by SHANTZ (22, pp. 182, 203). When, however, the height of the small trunks in the middle of a clump becomes too great for the animals to reach the top leaves, their safety is assured. In these taller growths the lower parts of the trees are much less dense; if there is no outer border of dense thicket, grazing animals are enabled to enter; the assemblage is now a scrubby forest of low trees, with open spaces between the trunks and very scanty undergrowth, as in fig. 6. Grazing animals may thus have a large part in determining the character and distribution of the oak vegetation.

#### CERCOCARPUS ASSOCIATION

CLEMENTS (1, p. 6) and SHANTZ (22, p. 179), foothill thicket formation, in part; RAMALEY (12, pp. 124-126), *Cercocarpus* shrub formation; RAMALEY and ROBBINS (15), local distribution in a square mile of rock ridge and foothills; SCHNEIDER (21, p. 292), thicket of south slopes, in part.

Ragged shrubs of *Cercocarpus parvifolius*, or, as it is called, mountain mahogany, form a characteristic vegetation in dry exposed rocky places, particularly along the mountain-front, on butte-slopes, hogback ridges, stony mesa-crests; in the foothills it is most abundant on south-facing side-slopes, or on the outermost slopes facing eastward on the plains. The stony fragments of the

<sup>4</sup> Either *L. Porteri* C. and R., or *L. affine* A. Nels., as determined by E. E. SHERFF.

soil vary from those of coarse granite-gravel to the variously sized blocks of rock talus.

The shrubs are 2-5 ft. high, very loose in habit, with few branches and reduced leaf surface. The fruits are provided with long plumed awns. The plants are separated, being regularly spaced like the pinyons, the intervals likewise varying with degree of exposure. The habitat relations of *Cercocarpus* are in fact quite like those of the pinyon, and it is north of the pinyon area that the mountain mahogany association is best developed. The interspaces



FIG. 6.—Open grove aspect of oak assemblage, caused by entrance of grazing animals, Perry Park; open mixed grassland in coarse soil occupies foreground.

between plants may be almost bare, or may be occupied by a sparse growth of xerophytes, most of them plains plants or representatives of the primitive grassland, the mat growth-form being common.

#### ARCTOSTAPHYLOS ASSOCIATION

COWLES (3, p. 367) and GATES (6, p. 306), Lake Michigan dunes; WHITFORD (26, p. 298), northern Michigan. In the Colorado foothills: ROBBINS (16, p. 44); SCHNEIDER (21, p. 299); SHANTZ (22, p. 186).

The *Arctostaphylos-Juniperus* association of the northeastern coniferous forest region is very well known to students of vegetation. Practically the same community is represented in the Rocky Mountains, associated there as elsewhere with coniferous vegetation. The same plant species and the same creeping habit are seen. The

important difference, as seen in the Front Range foothills, is that the juniper is very infrequently seen, the *Arctostaphylos* mostly dominating alone.

Conditions of soil-moisture, soil-texture, position, slope, and exposure are varied. The creeping mats of bearberry are seen on rock, in gravelly decomposed granite, and in fine moist humous soil; on practically all slopes, shaded and sunny, and through a considerable range in altitude. The growth is more extensive and more frequent, however, away from the mountain-front, at elevations 800-1200 ft. above the lower limit of rock pine, being increasingly abundant from that height upward, and being perhaps more typical of montane than of foothills vegetation. Its most frequent habitat in the foothills is the rolling floor of the granitic upland, the soil of which is thin, coarse, mostly compacted (granite-gravel). Here the conspicuous vegetation is rock pine, in open array of scattered clumps and single trees. Parts of the treeless surface are occupied by large mats of *Arctostaphylos*, with admixture of *Ceanothus Fendleri* (less of this upward); the rest of the area is bare or nearly so, with a few scattered herbaceous plants, mostly of primitive grassland.

#### CEANOTHUS ASSOCIATION

ROBBINS (16, p. 41); WATSON (25, p. 207).

The spiny shrub, *Ceanothus Fendleri*, is ecologically similar to *Arctostaphylos* in many respects. It forms a low, matlike, spreading ground cover, and occurs to some extent in mixture with bearberry mats. It differs from the other in being typical of more exposed and xerophytic slopes, in being abundant at lower altitudes, and more southerly in geographic distribution. MILLARD S. MARKLE informs the writer that the *Ceanothus* community is important in the Sandia Mountains of New Mexico, occurring frequently with the oaks and with *Robinia neo-mexicana*. *Ceanothus* ranges into dry fine-soiled habitats more frequently than *Arctostaphylos*, and is closely associated with grassland, rather than pine forest. It is not evergreen.

*Ceanothus* shrubs occur in closely set or scattered patches, mostly in unstable gravelly or finer soil of detrital slopes. They have a strongly accelerative part in vegetation-development. Their numerous twigs and thorns, even in the leafless winter condition, catch and hold wind-blown and washed-down soil particles and bits of plant debris, thus stabilizing and adding to the soil, and accumulating humus. In one station this had even resulted in the building of small dunes of wind-blown dust, of about 8 inches height and 18 inches diameter. Seed burial is favored in these mats, as well as germination. Some of the more mesophytic of the foothills plants are seen growing up through the tangled branches; pine seedlings also germinate in the shelter of *Ceanothus*, which may thus be an important factor in reforestation. On dry, burnt slopes *Ceanothus* frequently covers a considerable proportion of surface and, with the *Rhus cismontana* shrub growth, is an important stage in succession after burns.

*Ceanothus mollissimus* and what appears to be *Ceanothus subsericeus* Rydb. occasionally occur with the spiny species, in the less xerophytic stations. *Ceanothus velutinus* is rare in the lower foothills, but is frequent at higher elevations and farther north. Herbs of the primitive grassland and mixed grassland commonly grow out from between the twigs of *Ceanothus Fendleri*, and to some extent are seen in the spaces between the mats.

#### FOOTHILLS MIXED GRASSLAND ASSOCIATION

CLEMENTS (1), ground-cover in the foothill thicket and pine formations, in part; RAMALEY (12), foothill sagebrush-grass formation; SCHNEIDER (21), half gravel slide formation, and grassland of north slopes; SHANTZ (22), *Bouteloua* formation, in part: its modified form at the mountain-front; VESTAL (24, p. 386), *Bouteloua* mixed consociates, as developed at the mountain-front; WATSON (25, pp. 209, 210), herbaceous ground-cover in the yellow pine association, and mountain "meadows."

The mixed grassland association normally develops from primitive grassland, one of its important features being the establishment of the dominant *Bouteloua oligostachya*, the grama grass of the plains. It thus differs from the primitive grassland in that (1) the ground cover is less open, though still generally xerophytic; (2) the soil is usually more stable (in most situations a physical cause, rather than the effect, of the more permanent vegetation); (3) the soil is more finely broken up, and to it may be added considerable humus; and (4) a number of plains, prairie, and foothill species absent or rare in the primitive grassland are established.

The assemblage is most heterogeneous, since the many plants include widely diverse ecological, geographic, and floristic types. Extreme xerophytes and relatively mesophytic plants, plants of widely varying growth-form and seasonal relations, of great difference in plasticity to environmental variation, in altitudinal and habitat range, may occur in the same small grassland area. This mixed vegetation is really very closely allied to the modified plains grassland mentioned as the *Bouteloua* mixed consociates of the short-grass association (24, p. 386). This is found in the mixed mesa soils of the mountain-front zone just outside the foothills. The conditions which would result in heterogeneity of the grassland vegetation are probably similar in the lower foothills to those of the mountain-front; some of these are given in the article cited (24, pp. 381, 382).

So many species occur regularly in the mixed grassland, and the variability in floristic composition in particular stations is so great, that a selected list of plants equally representative of various localities and habitats cannot be

given. By way of illustration, however, a list of the plants observed in a particular mixed grassland station may be presented, and this is followed by a list of some other species commonly found in the community, but which happen to have been absent from the station selected. The station is on the east slope, not far from the top, of a hill a little over two miles west of the mountain-front and a little north of Boulder, in section 36, T 2 N, R 72 W. The hill is marked in the Boulder quadrangle of the United States topographic atlas by the altitude of its summit, 7168 ft. The spot studied most in detail is at about 7000 ft.; exposure is considerable, as the slope is even and treeless; drainage is probably quite rapid; the soil coarse, with but little humus; proportion of bare surface about 15 per cent on June 18, when the list was made. All of the plants marked as abundant or frequent occur in practically every square meter of surface.

PLANT COMPOSITION OF A TYPICAL MIXED GRASSLAND STATION

<i>Bouteloua oligostachya</i> (a)	<i>Eriogonum umbellatum</i> (i)
<i>Phacelia heterophylla</i> (a)	<i>Opuntia polyacantha</i> (i)
<i>Chrysopsis villosa</i> (?) (a)	<i>Oreocarya virgata</i> (i)
<i>Senecio oblancheolatus</i> (a)	<i>Artemisia gnaphalodes</i> var. (i)
<i>Geranium Parryi</i> (a)	<i>Astragalus flexuosus</i> (i)
<i>Artemisia frigida</i> (a)	<i>Eriocoma cuspidata</i> (i)
<i>Aragallus Lambertii</i> (a)	<i>Mamillaria vivipara</i> (i)
<i>Koeleria cristata</i> (f)	<i>Sitanion brevifolium</i> (i)
<i>Lesquerella montana</i> (f)	<i>Gaillardia aristata</i> (i)
<i>Mertensia lanceolata</i> (f)	<i>Phlox multiflora</i> (i)
<i>Linum Lewisii</i> (f)	<i>Potentilla pennsylvanica strigosa</i> (i)
<i>Carex pennsylvanica</i> (f)	<i>Euphorbia robusta</i> (i)
<i>Gilia pinnatifida</i> (lf)	<i>Aletes acaulis</i> (i)
<i>Gilia spicata</i> (lf)	<i>Poa longipedunculata</i> (i)
<i>Helianthus pumilus</i> (lf)	<i>Eriogonum alatum</i> (i)
<i>Cerastium arvense</i> (lf)	<i>Townsendia exscapa</i> (i)
<i>Aragallus albiflorus</i> (lf)	<i>Townsendia grandiflora</i> (i)
<i>Stipa comata</i> (lf)	<i>Allium</i> sp. (i)

The order in which the species are listed gives a rough approximation of their relative importance as making up a part of the vegetation, in descending scale. The names of plant species elsewhere frequent in the association follow:

ADDITIONAL SPECIES FREQUENT IN MIXED GRASSLAND

<i>Woodsia oregana</i>	<i>Echinocereus viridiflorus</i>
<i>Selaginella</i> , two spp.	<i>Gaura coccinea</i>
<i>Aristida longiseta</i>	<i>Cymopterus acaulis</i>
<i>Muhlenbergia gracillima</i>	<i>Gilia aggregata</i> et spp.
<i>Poa crocata</i>	<i>Lithospermum multiflorum</i>

<i>Poa Fendleriana</i>	<i>Onosmodium occidentale</i>
<i>Agropyron Smithii</i>	<i>Pentstemon humilis</i> et spp.
<i>Elymus triticoides</i>	<i>Castilleja integra</i> et spp.
<i>Leucocrinum montanum</i>	<i>Campanula rotundifolia</i>
<i>Calochortus Gunnisonii</i>	<i>Liatris punctata</i>
<i>Yucca glauca</i>	<i>Grindelia squarrosa</i>
<i>Zygadenus intermedius</i>	<i>Chrysopsis</i> spp.
<i>Comandra pallida</i>	<i>Solidago</i> spp.
<i>Allionia linearis</i> et spp.	<i>Aster</i> spp.
<i>Pulsatilla hirsutissima</i>	<i>Machaeranthera aspera</i> et spp.
<i>Argemone intermedia</i>	<i>Erigeron</i> spp.
<i>Corydalis aurea</i>	<i>Ratibida columnaris</i>
<i>Draba</i> spp.	<i>Helianthus</i> spp.
<i>Erysimum asperum</i>	<i>Hymenopappus filifolius</i>
<i>Potentilla</i> spp.	<i>Hymenoxys floribunda</i>
<i>Astragalus</i> spp.	<i>Artemisia aromatica</i>
<i>Psoralea tenuiflora</i>	<i>Artemisia canadensis</i>
<i>Malvastrum coccineum</i>	<i>Senecio plattensis</i> et spp.
<i>Viola Nuttallii</i>	<i>Senecio spartioides</i>
<i>Mentzelia</i> spp.	<i>Nothocalais cuspidata</i>

As regards distribution of the mixed grassland association in the foothills, it may be said that the primitive grassland is more frequent and occupies areas of greater extent, because of the general instability and rocky character of the sloping surfaces. In the upper foothills mixed grassland is absent from compacted soil level or rolling surfaces generally occupied by pine and *Arctostaphylos*, etc., but dominates on the more exposed mountain sides, which are treeless. The mixed grassland, like primitive grassland, is subject to a gradual ecological and floristic variation, from the south northward, and from the short-grass of the plains to the montane dry grassland of elevations from 8500 to 10,000 ft.

#### BUNCH-GRASS ASSOCIATION

CLEMENTS (1, p. 6), *Andropogon*, etc.; SCHNEIDER (21), half gravel slide formation, in part; SHANTZ (22, p. 43), *Bouteloua hirsuta* consociates, with *Andropogon* spp., *Atheropogon*, etc.; VESTAL (24, pp. 388–390), bunch-grass association: photograph and citation to descriptions in other regions; WATSON (25, p. 209), *Andropogon*, etc.

The bunch-grass vegetation of the foothills is quite similar to that of the mountain-front and over the whole prairie region, including most of the same species, but containing in addition other grasses of similar growth-form but of different geographic distribution. With the bunch-grasses are many composites and other



plants of the mixed grassland, such as *Liatris*, *Chrysopsis*, *Eriogonum alatum*, etc. The tufted bunch-grass growth-form is well known; the roots are deep and numerous; the plants are mostly late in flowering; they are active during the whole growing season, depending on a constant moisture supply. The chief habitats in the foothills which satisfy this condition are rocky or very coarse gravelly slopes, exposed and dry at the surface, but with rather more moisture beneath than in most areas of mixed grassland; these situations are consequently rather locally developed only.

#### PRAIRIE BUNCH-GRASSES OCCURRING IN FOOTHILLS

<i>Andropogon scoparius</i> (a)	<i>Muhlenbergia gracilis</i> (f)
<i>Andropogon furcatus</i> (a)	<i>Sporobolus heterolepis</i> (lf)
<i>Hilaria Jamesii</i> (li)	<i>Atheropogon curtispendus</i> (f)
<i>Sorghastrum nutans</i> (lf)	<i>Koeleria cristata</i> (f)

#### OTHER FOOTHILLS PLANTS OF BUNCH-GRASS TYPE

<i>Trisetum montanum</i> (l)	<i>Agropyron spicatum</i>
<i>Festuca confinis</i> (l)	<i>Sitanion longifolium</i>
<i>Agropyron occidentale</i> (l)	(?) <i>Elymus triticoides</i>

*Hilaria* is a southern plant and has not been seen north of about Canyon City. *Sorghastrum* and *Hilaria* appear not to extend far into the foothills. *Koeleria* ranges into many widely varying habitats and is found with many different plant assemblages. This may partly be due to its early ripening (it flowers in June), which may allow it to escape the dryness of the latter part of the season. Most of the plants of the second group bloom in early summer also; they are frequently found in clumps of one species, in rock crevices or coarse soils. *Trisetum* ranges into the montane zone, but not into the plains; it is restricted to moister places than most of the others. *Agropyron spicatum* is one of the chief dominants of the extensive grassland areas in the northwestern states, in intermontane valleys and the Columbia Basin plains. It too matures early in summer and is dried up the rest of the season. *Elymus triticoides* is included with some hesitation; it may be more like the grasses of the primitive bunch-grass type (24, p. 397).

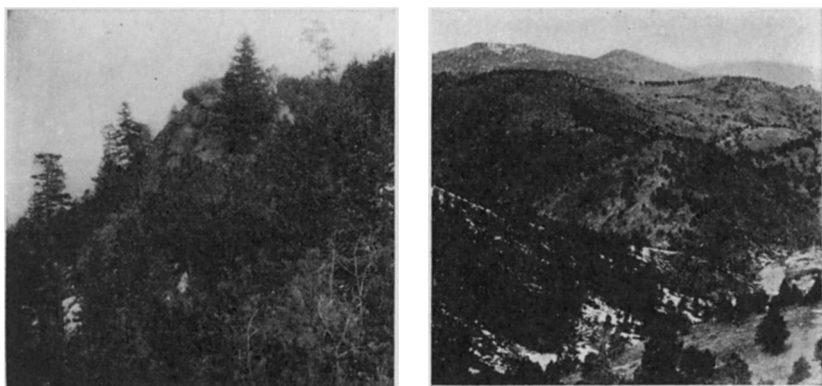
#### PSEUDOTSUGA ASSOCIATION

CLEMENTS (1, p. 14); SCHNEIDER (21, pp. 299, 300), with list of herbaceous plants; RAMALEY (14, pp. 251, 262); WATSON (25, p. 211); YOUNG (28, p. 343).

The Douglas "spruce," *Pseudotsuga mucronata*, is, like the rock pine, one of the most abundant and widely distributed conifers of

western North America, but in the foothills of the Front Range in Colorado it is relatively very local in occurrence. It is frequent only on north-facing slopes and in canyons, where the snow lies deep and late. It grows in close stands or as scattered trees (fig. 7).

Small trees of *Juniperus scopulorum* may occur infrequently in the *Pseudotsuga* forest; in unshaded areas with moist soil a few aspens may be found. *Arctostaphylos* and the prostrate *Juniperus communis sibirica*, so frequently associated with it, are seen as relics. The moist and sheltered slopes on which *Pseudotsuga* grows may in its stead be covered by the mesophytic grassland association, and many of its plants occur scattered among the conifers, such as



FIGS. 7, 8.—Fig. 7, *Pseudotsuga* association on a north slope; fig. 8, another general view, showing prevalence of grassland on side-slopes; trees conspicuous in profiles of distant slopes.

*Mertensia* spp., *Campanula rotundifolia*, *Pulsatilla hirsutissima*, *Saxifraga rhomboidea*, *Aster laevis*, and one or two small ferns.

The rock pine grows well in the moist habitats of the *Pseudotsuga*, if the young trees can get a start, and so the two species are commonly found in mixture, especially toward the top of canyon-slopes and in other less protected places. Also *Pseudotsuga* can range into the habitats of the pine, where, however, it is usually of less symmetrically spire-shaped form, and with fewer and uneven branches, so that the growth habit resembles that of the pine.

#### POPULIS-SALIX STREAM-SIDE ASSOCIATION

RAMALEY (12, p. 127, 14), part of the canyon forest formation; WATSON (25, p. 21), *Populus angustifolia* society; YOUNG (28, pp. 330–336).

The poplars and willows of stream-sides form a nearly continuous belt in the wider and more open canyon-bottoms of the foothills. *Populus angustifolia*,

the narrow-leaved cottonwood, is the largest and most frequent species. The willows include *Salix irrorata* and *S. exiguus*, forming shrubby clumps; and *S. Bebbiana*, *S. amygdaloides*, and *S. lasiandra*, small trees. The hackberry, *Celtis reticulata*, is perhaps more typically found scattered along stream-sides in quite exposed places than with other trees. It is also common in such habitats in New Mexico. Certain plants common in the canyon forest are also quite characteristic, in the rather less exposed stream-side situations, replacing the cottonwoods and willows in small areas, or intermingling with them. Such plants are *Alnus tenuifolia*, *Betula fontinalis*, *Acer Negundo*, and the shrubby *Cornus stolonifera*. Scattered plants of the mixed shrub association are also frequently seen: *Bossekia*, *Ribes*, *Rosa*, *Crataegus*, *Prunus demissa*, and others.

#### CANYON FOREST ASSOCIATION

RAMALEY (12, p. 127); YOUNG (28, pp. 333, 335), *Alnus-Betula-Corylus* assemblage; (*l.c.*, p. 334), *Crataegus* assemblage, etc.; DANIELS (4, pp. 21, 27).

The canyon forest, which contains many of the deciduous tree species of the foothills, is typically developed in local mesophytic stations, such as the slopes and bottoms of narrow canyons, in which the soil is moist (usually from seepage), and the air comparatively humid, due to the shade and the shelter from wind. A selected list of species is here given:

#### PLANTS OF FOOTHILLS CANYON FOREST ASSOCIATION

##### *Trees*

<i>Alnus tenuifolia</i>	<i>Prunus americana</i>
<i>Betula fontinalis</i>	<i>Prunus demissa</i> (Nutt.) Dietr. <sup>5</sup> ( <i>ch</i> )
<i>Salix Bebbiana</i> ( <i>i</i> )	<i>Robinia neomexicana</i> ( <i>l</i> )
<i>Populus tremuloides</i> ( <i>li</i> )	<i>Acer glabrum</i> ( <i>ch</i> )
<i>Amelanchier alnifolia</i> ( <i>li</i> )	<i>Acer Negundo</i> ( <i>l</i> )
<i>Prunus pennsylvanica</i> ( <i>ch</i> )	<i>Crataegus coloradensis</i> et spp.

##### *Shrubs*

<i>Corylus rostrata</i> ( <i>l</i> )	<i>Rhus Rydbergii</i> ( <i>i</i> )
<i>Ribes longiflorum</i>	<i>Vitis vulpina</i> ( <i>l</i> )
<i>Physocarpus Ramaleyi</i> ( <i>i</i> )	<i>Parthenocissus vitacea</i> ( <i>l</i> )
<i>Rosa Sayi</i> et spp.	<i>Viburnum pauciflorum</i> ( <i>li</i> )

<sup>5</sup> JONES (8, p. 35) fails "to see any ground for NELSON's *P. melanocarpa*, even though NUTTALL describes his as red-fruited, for we know that this species has fruit red till dead ripe, when it turns black."

*Herbs*

<i>Pteridium aquilinum</i>	<i>Fragaria pauciflora</i> et spp.
<i>Smilacina stellata</i> (ch)	<i>Aralia nudicaulis</i>
<i>Smilacina amplexicaulis</i> (ch)	<i>Viola canadensis</i> Rydbergii (ch)
<i>Stellaria Jamesiana</i>	<i>Castilleja miniata</i> et spp.
<i>Thalictrum</i> spp.	<i>Monarda Ramaleyi</i> et spp.
<i>Aquilegia coloradensis</i>	<i>Hydrophyllum Fendleri</i> (ch)
<i>Delphinium Nelsonii</i> (ch)	<i>Galium boreale</i> (ch)
<i>Ligusticum Porteri</i> (?)	<i>Galium aparine</i>
<i>Saxifraga rhomboidea</i> (ch)	<i>Galium Vaillantii</i>

The canyon forest presents a wide range of variability, according as favorable ground conditions are uniform or interrupted; thus in rocky canyon-bottoms and slopes it is patchy in development. It may merge into, or mingle with, areas of *Pseudotsuga*, mixed shrub, aspen, *Populus-Salix*, *Quercus*, and moist grassland growths. The herbs especially may be no more typical of unmixed mesophytic deciduous forest than of many other mesophytic habitats. The characteristic plants growing in the shade of large shrubs and trees are *Viola*, *Hydrophyllum*, and one or more species of *Galium*. These are abundant in unmixed canyon forest, at least in the northern foothills.

*Amelanchier* is an important component only in the upper foothills and the montane zone, or farther north and west in the Rocky Mountains. *Acer glabrum* often occurs by itself on north or shaded slopes, the bushy plants 10-15 ft. in height, and in most places considerably separated. *Prunus demissa*, and several species of *Crataegus* (mostly *C. coloradensis* and *C. ceronis*), together or singly, dominate tall thickets or low forests, which may be regarded as transitional between the mixed shrub and canyon forest associations. In new growths or exposed situations they are low and scrubby; in other places they form a taller and closed growth, with a lower stratum of mesophytic herbs, and may properly be spoken of as forest. *Prunus demissa* and *Crataegus* form relatively much more extensive areas of vegetation in the northern foothills and especially along the northern mountain-front than in the southern part of Colorado. *Robinia* is abundant in the southern third of the foothills area. It ranges into drier habitats, in which it is low and scrubby.

The *Alnus-Betula* consociates has been mentioned as being abundant along mesophytic stream-sides. *Corylus* is frequent only in such situations, occurring in places alone, in others with *Alnus* and *Betula*. The climbers, clematis, Virginia creeper, and grape, are local, and more common in sunny openings. *Viburnum* is in moist canyon-bottoms of the higher foothills.

## ASPEN ASSOCIATION

RAMALEY (14, p. 251); YOUNG (28, p. 347).

Botanists are familiar with the rôle of *Populus tremuloides* in revegetation of burned areas, and it is prominent in the montane zone in Colorado in this capacity. The general area of the lower foothills, however, is too dry for establishment of aspens, and they occur only locally, in ravines even more mesophytic, perhaps, than the ordinary habitat of the canyon forest. Thus in the Boulder area the stations below 7200 ft. in which aspens have been observed in local abundance are very infrequent. Such stations are usually in sheltered ravines with deep humous soil, abundantly moist. The trees in places are large, the undergrowth very mesophytic, with *Thalictrum*, *Heracleum*, *Castilleja* spp., etc., and particularly *Aquilegia coerulea*. At about 7800 ft. in the same vicinity aspens begin to appear in small clumps on the granite-gravel upland, among more frequent clumps of rock pines. No connection with former fires could here be made out; appearances indicated that perhaps there the aspens might be associated with the moist patches resulting from the tardy disappearance of the deeper snowdrifts of winter. The conspicuous yellow color of the aspens in fall probably tends to exaggerate the popular notion of their frequency of occurrence.

## MIXED SHRUB ASSOCIATION

DANIELS (4, p. 20); RAMALEY (12, p. 127), shrubs of the canyon forest; SHANTZ (22, p. 179), thicket formation, in part; notes on distribution and ecological relations of the species; RAMALEY (11); ROBBINS (16); SCHNEIDER (20).

The shrub associations of the foothills, like the deciduous tree growths, are generally found in rocky or coarse soil stations with constant moisture supply in the substratum, which is reached by the deep root systems. Local distribution, as in the case of the pines, is probably restricted by unfavorable conditions for germination over a large part of the general area. It has been observed that, on irregular slopes where the distribution of snow in late spring is uneven, the shrubs occupy the moister spots determined by the deeper snow patches. In deep moist soil it is likely that the shrubs are soon succeeded by trees, as has been observed in some stations. The shrub species most commonly found appear in the following selected list. Certain of the canyon forest plants which occur with the shrubs in the less mesophytic stations without attaining tree size are included here also. It is significant that so many of the

shrubs, and some of the canyon forest plants, have fleshy fruits, and so may be distributed by birds.

PLANTS OF FOOTHILLS MIXED SHRUB ASSOCIATION

<i>Ribes saxosum</i>	<i>Rosa arkansana</i>
<i>Ribes pumilum</i>	<i>Rosa Fendleri</i>
<i>Ribes vallicola</i>	<i>Amelanchier alnifolia</i> (i)
<i>Ribes longiflorum</i> (l)	<i>Crataegus cernonis</i>
<i>Jamesia americana</i> (l)	<i>Crataegus coloradensis</i>
<i>Holodiscus dumosus</i> (l)	<i>Prunus americana</i> (ch)
<i>Physocarpus intermedius</i> (l)	<i>Prunus demissa</i> (ch)
<i>Physocarpus monogynus</i> (l)	<i>Robinia neo-mexicana</i> (l)
<i>Bossekia deliciosa</i> (f, ch)	<i>Rhus trilobata</i> (ch)
<i>Rubus strigosus</i> (l)	<i>Ceanothus subsericeus</i>
<i>Rosa Sayi</i>	

*Amelanchier* has been mentioned as being rare in the northern foothills, as may be said also for *Holodiscus*. The common shrubs of rock-crevice habitats are *Jamesia* and *Ribes pumilum*. The yellow-flowered *Ribes longiflorum*, unlike the others of the genus, is more frequent in deep, moist, fine-grained soil than in rocky or coarse soil. *Rubus strigosus* is more common in the upper foothills, and in less exposed habitats. It and the roses are smaller than most of the other shrubs. *Prunus americana* forms low dense thickets in rather exposed places. *Robinia* is southern. *Rhus trilobata* ranges into very xerophytic habitats, and can persist and even establish itself on unstable soil of steep or loose slopes. Although a single species may make up the shrub vegetation at any one spot, numbers of them occur together in a very large variety of combinations, particularly where the habitat is internally diverse. The *Cercocarpus*, *Symphoricarpos*, *Ceanothus Fendleri*, sumac, and bearberry associations, on the other hand, show rather constant differences in environmental relations and distribution from the various representations of the mixed shrub association, and consequently have been separated from it. The relation of the mixed shrub association to the canyon forest has already been mentioned; the two grade into each other, but in the main they are quite distinct.

Where the shrubs grow close together, a mesophytic undergrowth of herbs develops. *Galium aparine* or *G. Vaillantii*, *Delphinium Nelsonii*, and *Viola canadensis Rydbergii* are frequent species. The border of many shrub areas, where there is no grazing, shows tall herbs, as *Lupinus*, *Achillea*, *Monarda*, *Pentstemon unilateralis*, etc. Surface rocks, where present in grassland, may allow the scattering admixture of a shrub element, or even, where the soil is sufficiently moist, invasion of shrubs over the general area.

## SYMPHORICARPOS ASSOCIATION

RAMALEY (12, pp. 127, 128); ROBBINS (16, p. 38).

The *Symphoricarpos* association is best developed in moist, fine-grained soil; best seen, in the foothills, on basal or other deep-soiled detrital slopes, clay or loam, with or without humus. The common species of the Colorado foothills is *Symphoricarpos occidentalis*. The bushes are low, are spaced very close together, and are profusely branched, giving the whole growth a very compact and uniformly dense structure, especially where subject to grazing, as in many stations. From its habitat relations, the bush honeysuckle, as it may be called (it is known in some localities as buckbrush), adjoins a semi-mesophytic grassland in most places, competing and alternating sharply with it. Many of the taller mesophytic herbs are seen at the border, including *Frasera speciosa*, *Thermopsis divaricarpa*, the others already mentioned as bordering canyon forest and mixed shrub, and frequently the tall grass *Stipa viridula*. This border condition is best seen where the *Symphoricarpos* assemblage occupies a depression.

The shrub area is dominated by the one species, although bushes of *Rosa arkansana* are mixed in, abundantly in places, and *Berberis aquifolia* may also be seen. A few herbs may occur underneath.

*Symphoricarpos* in places forms a border between mixed shrub or canyon forest vegetation and grassland.

## MESOPHYTIC GRASSLAND ASSOCIATION

RAMALEY (12, p. 129), meadow formation.

There are several kinds of herbaceous vegetation in the foothills, of mesophytic or semi-mesophytic character, which may for convenience be considered together. There is a meadow growth, which shades more or less completely into the western prairie-grass of the mountain-front (24, p. 390), on the one hand, and into the forest border and forest undergrowth assemblages on the other. On certain shaded ravine slopes a mixture of mesophytic herbs from several of these assemblages has been observed, apparently independent of any tree canopy. The trees affect the herbs, apparently, mainly or wholly by their modification of physical conditions. A selected list of mesophytic and semi-mesophytic species may be given:

## MESOPHYTIC AND SEMI-MESOPHYTIC HERBS OF FOOTHILLS

<i>Stipa viridula</i> (ch)	<i>Gentiana affinis</i>
<i>Danthonia Parryi</i> (f)	<i>Frasera speciosa</i> (ch)
<i>Poa pratensis</i>	<i>Mertensia ciliata</i>
<i>Poa Buckleyana</i>	<i>Mertensia lanceolata</i>
<i>Agropyrum violaceum</i>	<i>Monarda menthaefolia</i> (ch)

<i>Calochortus Gunnisonii</i>	<i>Pentstemon humilis</i> ( <i>la</i> )
<i>Zygadenus intermedius</i> ( <i>ch</i> )	<i>Pentstemon unilateralis</i>
<i>Iris missouriensis</i> ( <i>li</i> )	<i>Castilleja linariaefolia</i> ( <i>ch</i> )
<i>Claytonia virginiana</i>	<i>Castilleja sulphurea</i>
<i>Cerastium arvense</i> ( <i>ch</i> )	<i>Orthocarpus luteus</i>
<i>Delphinium Nelsonii</i> ( <i>ch</i> )	<i>Galium boreale</i> ( <i>ch</i> )
<i>Thlaspi coloradense</i> ( <i>l</i> )	<i>Campanula rotundifolia</i>
<i>Erysimum Wheeleri</i> ( <i>ch</i> )	<i>Aster laevis</i>
<i>Saxifraga rhomboidea</i> ( <i>ch</i> )	<i>Erigeron flagellaris</i>
<i>Potentilla pennsylvanica strigosa</i> ( <i>ch</i> )	<i>Achillea millefolium</i>
<i>Thermopsis divaricarpa</i> ( <i>ch</i> )	<i>Arnica cordifolia</i>
<i>Lupinus argenteus</i> et spp.	<i>Arnica fulgens</i> ( <i>la</i> )
<i>Lathyrus leucanthus</i>	<i>Senecio integerrimus</i> ( <i>la</i> )
<i>Viola canadensis Rydbergii</i>	

The prairie grass aspect has already been mentioned, and a description cited. The foothill meadow assemblage in early summer typically shows such conspicuous plants as *Delphinium*, *Cerastium*, *Arnica*, *Senecio*, and *Castilleja linariaefolia* (*C. sulphurea* is frequent only in the higher elevations). The mixed shrub association frequently alternates with meadow, and encroaches upon it, and is bordered by the taller herbs with that assemblage. The forest border and forest undergrowth communities have also been mentioned.

Moist rock crevices in sheltered ravines become overgrown with cushions of *Selaginella* (fig. 2) and smaller cushions of mosses; humus accumulates by the growth and death of these plants; in this *Saxifraga rhomboidea* and later other herbaceous or woody plants may become established. This is a very common successional series from bare rock in mesophytic habitats.

Herbaceous plants commonly seen scattered along the moist soil of stream margins, in open situations, include *Rumex* sp., *Heracleum lanatum*, *Thermopsis*, and *Lupinus*, with certain grasses, as *Muhlenbergia racemosa*, *Eatonia obtusata*, etc.

Hygrophilous and amphibious plants of the canyon streams may for convenience be mentioned at this point. *Marchantia polymorpha* is found on a very few stream margins on rocks or in crevices in sheltered spots. Many mosses may accompany it, especially where some soil accumulates in cracks of stream-side boulders, etc. *Dodecatheon radiculatum* may here be found, or species of *Ranunculus* in boggy places. A number of species are seen in these very restricted boggy places. *Mimulus Langsdorfii* and *Veronica americana* may grow there or in quiet little pools of the stream itself. RAMALEY has given these growths the name Stream Bank Marsh Society (12, p. 127).



## LITERATURE CITED

1. CLEMENTS, F. E., Formation and succession herbaria. Univ. Neb. Studies 4:329-355. 1904.
2. COULTER, J. M., and NELSON, A., New manual of botany of the Central Rocky Mountains. New York. 1909.
3. COWLES, H. C., The ecological relations of the sand dunes of Lake Michigan. BOT. GAZ. 27:95, 167, 281, 361. 1899.
4. DANIELS, F. P., The flora of Boulder, Colorado, and vicinity. Univ. Mo. Studies 2 (Science Series): no. 2; pp. xiv+311. 1911.
5. DAVIS, W. M., The Colorado Front Range. Ann. Ass. Am. Geog. 1:21-83. 1911.
6. GATES, F. C., The vegetation of the beach area in northeastern Illinois and southeastern Wisconsin. Bull. Ill. State Lab. Nat. Hist. 9:251-372. 1912.
7. HERRE, A. W. C. T., The lichens of Mount Rose, Nevada. BOT. GAZ. 55:392-396. 1913.
8. JONES, M. E., Montana botany notes. Univ. Mont. Bull. no. 61 (Biol. Series no. 15), pp. 1-75. 1910.
9. POUND, R., and CLEMENTS, F. E., The phytogeography of Nebraska. 2d ed. Lincoln. pp. 442. 1900.
10. RAMALEY, F., Plant zones in the Rocky Mountains of Colorado. Science 26:642-643. 1907.
11. ———, Woody plants of Boulder County. Univ. Colo. Studies 5:47-63. 1907.
12. ———, Botany of northeastern Larimer County, Colorado. Univ. Colo. Studies 5:119-131. 1908.
13. ———, Climatology of the mesas near Boulder. Univ. Colo. Studies 6:19-31. 1908.
14. ———, Forest formations and forest trees of Colorado. Univ. Colo. Studies 6:249-281. 1909.
15. RAMALEY, F., and ROBBINS, W. W., Ecological notes from north-central Colorado. Univ. Colo. Studies 5:111-117. 1908.
16. ROBBINS, W. W., Distribution of deciduous trees and shrubs on the mesas. Univ. Colo. Studies 6:36-49. 1908.
17. ———, Climatology and vegetation in Colorado. BOT. GAZ. 49:256-280. 1910.
18. ROBBINS, W. W., and DODDS, G. S., Distribution of conifers on the mesas. Univ. Colo. Studies 6:31-36. 1908.
19. RYDBERG, P. A., Flora of Colorado. Bull. 100, Exp. Sta. Colo. Agr. Coll. Fort Collins. pp. 448. 1906.
20. SCHNEIDER, E. C., The distribution of woody plants in the Pike's Peak region. Colo. Coll. Publ., Science Series 12: no. 6; pp. 137-170. 1909.
21. ———, The succession of plant life on the gravel slides in the vicinity of Pike's Peak. Colo. Coll. Publ., Science Series 12: no. 8; pp. 289-311. 1911.

22. SHANTZ, H. L., A study of the vegetation of the mesa region east of Pike's Peak: The *Bouteloua* formation. BOT. GAZ. 42:16-47, 179-207. 1906.
23. TUCKERMAN, E., List of species of lichens collected by the Wheeler Survey. U.S. Geog. Surv. 6:350, 351. 1878.
24. VESTAL, A. G., Prairie vegetation of a mountain-front area in Colorado. BOT. GAZ. 58:377-400. 1914.
25. WATSON, J. R., Plant geography of north-central New Mexico. BOT. GAZ. 54:194-217. 1912.
26. WHITFORD, H. N., The genetic development of the forests of northern Michigan. BOT. GAZ. 31:289-325. 1901.
27. WILLIAMS, T. A., Lichens of the Black Hills and their distribution. Bull. Torr. Bot. Club 20:349-355. 1893.
28. YOUNG, R. T., The forest formations of Boulder County, Colorado. BOT. GAZ. 44:321-352. 1907.